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***CTENACIS* AND *GOLLUM*, TWO NEW
GENERAL OF SHARKS
(SELACHII; CARCHARHINIDAE)**

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ABSTRACT: Two new genera are described for two species of carcharhinid sharks formerly placed in *Triakis* Müller and Henle. *Ctenacis*, new genus, is proposed for *Triakis fehlmanni* Springer, 1968. *Gollum*, new genus, is proposed for *Triakis attenuata* Garrick, 1954. Both genera are closest to *Proscyllium* Hilgendorf and *Eridacnis* H. M. Smith within the Carcharhinidae. *Ctenacis* is most similar to *Eridacnis* and somewhat less so to *Proscyllium*. *Gollum* is more distant from *Proscyllium*, *Ctenacis*, and *Eridacnis* than the latter three genera are from each other.

Garrick (1954) described a peculiar new shark, *Triakis attenuata*, that in many features differs strikingly from typical species of that genus. Subsequent workers on *Triakis*, as Smith (1957), Kato (1968), and Springer (1968), accepted Garrick's generic placement of 'attenuata.' In addition, Springer (1968) described another new species of *Triakis*, *T. fehlmanni*, that also differed greatly from the type-species, *T. scyllum*, and its closest relatives. Springer regarded the generic position of 'fehlmanni' as provisional pending a revision of *Triakis*.

Compagno (1970) proposed a preliminary reorganization of *Triakis*. He removed *T. leucoperiptera* from *Triakis* and assigned it to the genus *Hemitriakis*. *Proscyllium* was resurrected for *T. habereri* and *T. venusta* and *Calliscyllium* were synonymized with it. *Eridacnis* and *Neotriakis* were previously synonymized with *Triakis* by Kato (1968), but Compagno revived *Eridacnis* for *E. radcliffei*, *Neotriakis sinuans*, and *Triakis barbouri*. *Neotriakis* was synonymized with *Eridacnis*. Following several previous workers, Compagno transferred *Triakis henlei* to *Mustelus*.

Triakis, as restricted by Compagno (1970), contained a group of closely

similar species, *T. scyllium*, *T. semifasciata*, *T. maculata*, and *T. acutipinna*, that seem to grade into *Mustelus* through intermediate forms as *M. nigropunctatus*, *M. megalopterus*, *M. henlei*, and *M. dorsalis*. *Triakis attenuata* was considered to be probably distinct from *Triakis* proper but inadequate data on the species at the time precluded more definite generic assignment. *Triakis fehlmanni* was treated as a doubtful appendage to *Eridacnis* that might merit generic or subgeneric distinction.

Reconsideration of available data on *T. fehlmanni* indicates that this species should be separated from *Eridacnis* and *Triakis* in a new genus. Examination of two specimens of *T. attenuata* confirmed my earlier opinion that 'attenuata' was generically distinct from *Triakis* and required a new genus also.

The terminology used here for external morphology, vertebral counts, and dentition is from Compagno (1970). Clasper terminology follows Leigh-Sharpe (1921) and Compagno and Springer (1971). Terms for vertebral calcification patterns are from Ridewood (1921). Cranial terms are modified from Gegenbaur (1872), Allis (1923), and Holmgren (1941).

Ctenacis Compagno, new genus

TYPE SPECIES. *Triakis fehlmanni* Springer, 1968.

DEFINITION. Head very broad, depressed, its length 23 percent of total length in adult. Head length greater than distance between pectoral and pelvic bases. Snout outline subparabolic in dorsoventral view, not bell-shaped. Snout short, length 6.5 percent of total length. Eyes high on sides of head, above level of nostrils by a space about equal to eye height. Subocular ridge very strong, not indented on its dorsal surface. Eyes not visible in ventral view of head. Eyes elongate-elliptical, about 2.5 times as long as high. Nictitating lower eyelid rudimentary, with its edge horizontal. Subocular pouch very shallow, with its interior surface covered with denticles.

Spiracles present, their length about 5 times in eye length. Shortest gill opening over $\frac{3}{4}$ as long as longest. Gill rakers present on gill arches.

Internarial space about 1.2 times nostril width. Anterior nasal flaps are broad, low, triangular lobes with fringed posterior edges, not elongated, barbel-like, or tubular. Posterior edges of anterior nasal flaps close to mouth but separated from level of upper symphysis by distance equal to $\frac{1}{3}$ of nostril width. Posterior nasal flaps large, with fringed edge. No nasoral grooves.

Mouth distinctly angular in shape, with edges of lower jaw nearly straight. Large papillae present in buccal cavity. Labial furrows extremely short, essentially confined to the mouth corners.

Diphycodont heterodonty weak, upper teeth with higher and narrower crowns than lowers at symphysis, lower teeth more comblike than uppers at ends of dental bands. No disjunct monognathic heterodonty. In both jaws teeth decrease in size and height relative to root width towards rictuses. In the lower

jaw premedial cusplets increase in size and number and the primary cusp shifts postlaterally on the crown base towards the rictus, producing comblike posterior teeth.

Tooth rows 86/88, series functional 4-5/5-7. Teeth not bladelike, without serrations or sharp edge. Premedial cusplets present on all teeth except a few in the region of the symphysis. Postlateral cusplets present on all teeth. Primary cusp present on all teeth, narrow, erect or slightly oblique. Crown foot with a strong basal ledge overlapping a deep basal groove. Transverse ridges present on all teeth, extending on to the cusps of uppers, confined to the bases in lowers. Roots of teeth broad, flat, low, platelike. No transverse groove and notch on attachment surface of roots. Teeth not extending onto sides and ventral surfaces of lower jaw.

No interdorsal ridge, lateral dermal keels on the caudal peduncle, or pre-caudal pits. Length of head and trunk (from snout tip to vent) about 46 percent of total length.

Denticles below first dorsal fin with crowns about as wide as long or slightly longer than wide in adult. Denticle crowns with a strong medial cusp and a pair of strong medial ridges; a pair of weaker lateral ridges are also present and a pair of very weak lateral cusps may be present or not.

Pectoral fin skeleton projecting about $\frac{1}{3}$ of pectoral anterior margin length into fin. Longest distal radials of pectoral much shorter than longest proximal ones. Distal pectoral radials with parallel edges and truncate tips.

Pelvic bases over twice as far from second dorsal base as from first dorsal base. Posterior margins, free rear tips, and posterior margins of pelvic fins not attenuate. Clasper morphology unknown.

Midpoint of first dorsal base about twice as far from pectoral bases as from pelvic bases. Free rear tip of first dorsal posterior to pelvic origins.

Second dorsal fin nearly as large as first, its height almost $\frac{1}{10}$ of height of first, its base length 1.2 times base length of first dorsal. Posterior margin of second dorsal weakly concave.

Anal fin much smaller than second dorsal, its height about half of second dorsal height, its base length about $\frac{3}{4}$ of second dorsal base length. Anal origin posterior to second dorsal origin by distance about $\frac{1}{4}$ of second dorsal base length. Anal insertion under second dorsal insertion. Posterior margin of anal straight.

Caudal fin without distinct ventral lobe, postventral caudal margin not notched or otherwise differentiated. Subterminal caudal margin about $\frac{4}{5}$ of terminal caudal margin. Caudal short, not tapelike, dorsal caudal margin 23 percent of total length. No lateral undulations in dorsal caudal margin. Terminal sector of caudal about 4 times in dorsal caudal margin. No caudal crest of denticles.

Cranium with paired lateral and unpaired medial rostral cartilages, fused

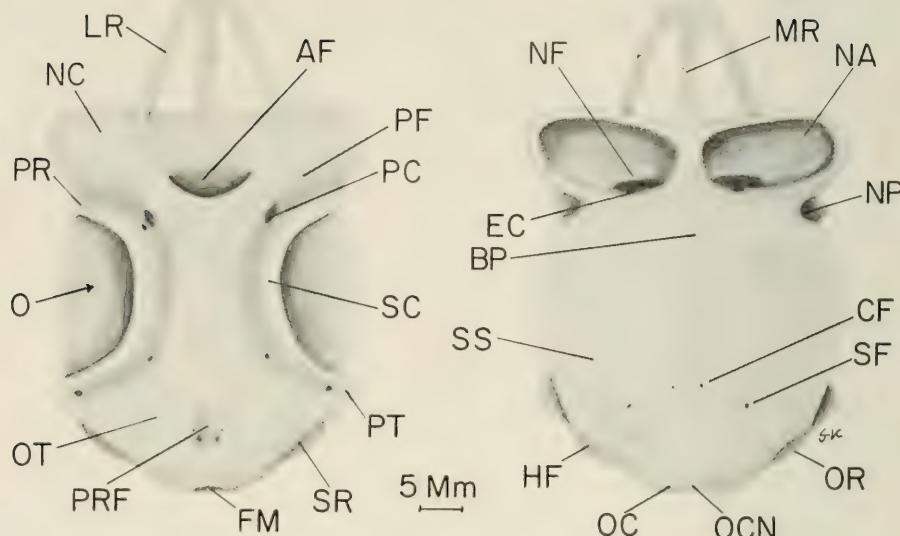


FIGURE 1. *Ctenacis fehlmanni*, U. S. National Museum 202969, 46 cm, adult female, neurocranium in dorsal (left) and ventral (right) views. Abbreviations: AF, anterior fontanelle; BP, basal plate; CF, internal carotid foramen; EC, ectethmoid chamber; FM, foramen magnum; HF, hyomandibular facet; LR, lateral rostral cartilage; MR, medial rostral cartilage; NA, nasal aperture; NC, nasal capsule; NF, nasal fontanelle; NP, notch for orbital process of palatoquadrate; O, orbit; OC, occipital condyle; OCN, occipital centrum; OR, opisthotic ridge; OT, otic capsule; PC, preorbital canal; PF, profundus foramen; PR, prerorbital process; PRF, parietal fossa; PT, postorbital process; SC, supraorbital crest; SF, stapedial foramen; SR, sphenopterotic ridge; SS, suborbital shelf.

at their tips to form a tripod (fig. 1). Rostral node (conjoined tips of rostral cartilages) not yokelike, not penetrated by a rostral fenestra. Rostrum fairly short, length of medial rostral cartilage from its base on the internasal septum to the anterior tip of the rostral node about three times in nasobasal length (distance from base of medial rostral cartilage to the posterior edge of the occipital centrum; here used as an independent variable for cranial proportions). Distance between bases of lateral rostral cartilages about equal to length of medial rostral cartilage. Lateral rostral cartilages with their bases far anterior to the anterior fontanelle and not connected to the dorsal edge of the fontanelle by a ridge.

Nasal capsules oval-shaped, their long axis transverse to the longitudinal axis of the cranium. Transverse width of capsule from internasal septum to lateral edge of capsule about twice its length across its anterior and posterior walls. Greatest transverse width across nasal capsules about 1.3 in nasobasal length. Nasal aperture and nasal fontanelle apparently broadly continuous with each other, the fontanelle not separated from the nasal aperture by a

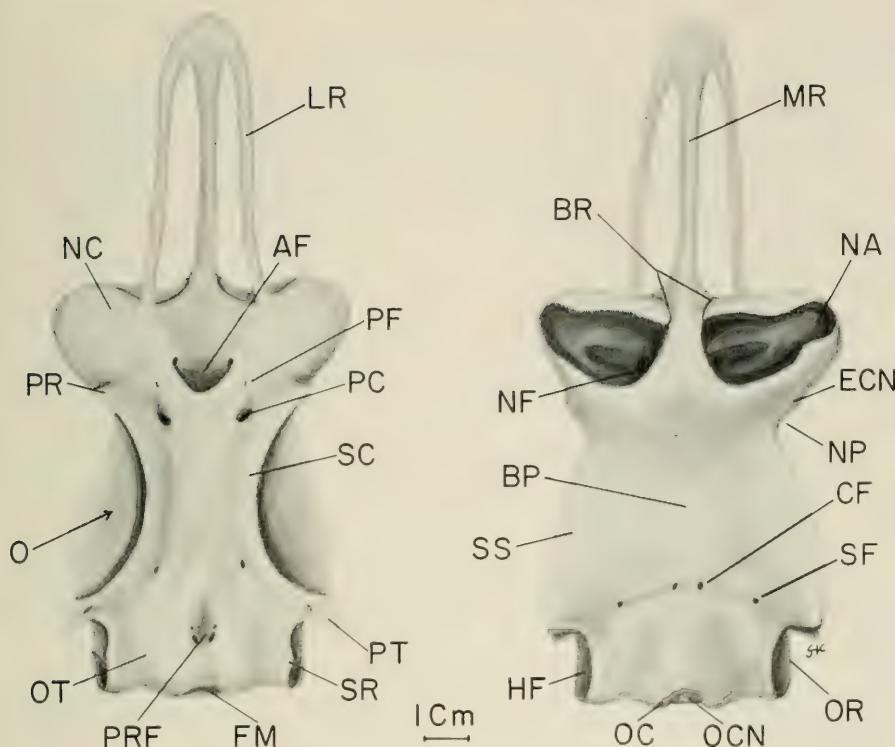


FIGURE 2. *Gollum attenuatus*, DM-3636, 955 mm. adult male, neurocranium in dorsal (left) and ventral (right) views. Abbreviations as in figure 1, except: BR, basirostral fenestra; ECN, lateral ectethmoid condyle.

bridge of cartilage. Greatest width of nasal aperture about six times distance between nasal apertures across internasal septum. Ectethmoid chamber opening inside nasal capsule on its posteroventral wall, with its aperture just above posterior edge of nasal fontanelle and not separated from the fontanelle by a horizontal ledge beneath it. No ectethmoid condyles or subethmoid fossa. No ectethmoid foramen communicating between the ventral surface of the nasal capsule and the ectethmoid chamber.

Anterior fontanelle subcircular in shape, its greatest width about 4.6 in nasobasal length. Cranial roof convex between orbits.

No deep notch separating anterior end of suborbital shelf from nasal capsule. Basal plate expanded just posterior to nasal capsules into a broad suborbital ledge, the least width across which is about 1.7 in nasobasal length. Arterial foramina on ventral surface of basal plate include a pair of small internal carotid foramina about half as far from each other as from each of the stapedial foramina distal to them. The paired stapedial foramina, for the

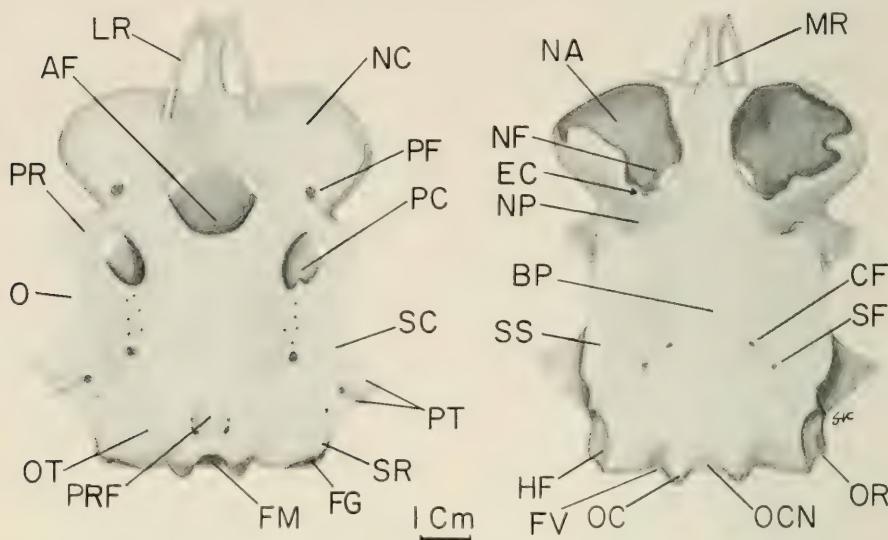


FIGURE 3. *Triakis semifasciata*, LJVC (writer's personal collection) 0067, 937 mm. immature female, neurocranium in dorsal (left) and ventral (right) views. Abbreviations as in figure 1, except: FG, foramen for glossopharyngeal (IX) nerve; FV, foramen for vagus (X) nerve.

stapedial or orbital arteries, are tiny pinhole apertures. Basal plate nearly flat, without keels.

Supraorbital crest present, connecting low preorbital and postorbital processes. Edge of supraorbital crest arcuate in dorsal view. Dorsal edge of crest not extending above level of cranial roof between the orbits. Width across narrowest part of supraorbital crest about 2.6 in nasobasal length. Postorbital processes not extending from supraorbital crest and sphenopterotic ridge, with tips not bifurcated. Suborbital shelf very wide, greatest width across it 1.3 in nasobasal length.

Otic capsules short, not greatly enlarged or inflated. Length of otic capsule about 4 in nasobasal length. Sphenopterotic ridge extending slightly lateral to side of otic capsule.

Occipital condyles very small, without dorsolateral and ventrolateral plates that partially sheath base of vagus nerve.

Total vertebral count 136 (1). Monospondylous precaudal (MP) centra 28.6, diplospondylous precaudal (DP) centra 35.2, and diplospondylous caudal (DC) centra 36 percent of total vertebral count. Ratio of DP/MP centra counts 1.23, DC/MP centra 1.26. "A" ratio (length of penultimate MP centrum/first DP centrum) 138, "B" ratio (length/width of penultimate MP centrum) 114. No 'stutter zone' of alternating long and short centra in DP region. Last few MP centra not greatly enlarged.

Vertebral centra without wedgelike intermedia. Diagonal calcified lamellae present in form of knoblike projections from calcified double cone. Notochordal canal rather large, not blocked at apices of double cone.

Spiral intestinal valve present, with about 10 turns.

Mode of development not known, though possibly oviparous (see Springer, 1968, for discussion).

A color pattern of dark saddles, blotches, bars, and spots on a light background present.

Size small, the one specimen of *C. fehlmanni* known at present being an adult female 46 cm. long.

COMPARISON WITH OTHER GENERA. *Ctenacis* is a member of Compagno's (1970) group of 'scyliorhiniform triakoids,' which are morphologically intermediate between scyliorhinids and genera such as *Triakis*, *Mustelus*, and *Hemitriakis*. *Ctenacis* is most similar to *Eridacnis*, somewhat less so to *Proscyllium*, and yet more distant from *Gollum*, the other new genus described here. All four genera show sufficient similarity in external morphology, dentition, cranial anatomy, and vertebral calcification pattern to form an apparently related group.

For brevity comparisons of both *Ctenacis* and *Gollum* with other carcharhinid genera is here limited to the other 'scyliorhiniform' genera and to *Triakis*-*Mustelus*, the generic complex to which 'fehlmanni' and 'attenuata' were originally assigned. Both genera are not particularly close to carcharhinid from these genera by many characters given in the generic definitions.

genera other than *Proscyllium* and *Eridacnis* and can be readily distinguished

Eridacnis differs from *Ctenacis* in having a narrower head; anterior and posterior nasal flaps not fringed; tooth rows less numerous, 55–78/63–77; head and trunk slightly shorter, 38–43 percent of total length, and rather slim; pelvic posterior margins, free rear tips, and inner margins elongate, somewhat attenuate; caudal very long, tapelike, length 25–30 percent of total length; cranium narrower, width across nasal capsules 1.4–1.6 in nasobasal length; nasal capsules nearly spherical; no diagonal calcified lamellae in vertebral centra; no striped and spotted color pattern on body; and size smaller, less than 370 mm. total length.

Proscyllium differs from *Ctenacis* in having a narrower and shorter head, with length only 16–18 percent of total length; fifth gill opening less than half length of third; anterior nasal flaps very large, reaching nearly to upper symphysis; internarial space very narrow, nostril width 1.7–2.2 times internarial; anterior and posterior nasal flaps not fringed; tooth rows less numerous, 46–62/49–59; head and trunk very short, only 39–41 percent of total length, very slender; first dorsal origin well posterior to free rear tip of pectoral; anal origin slightly anterior to second dorsal origin; cranium narrower, width across nasal capsules 1.5 in nasobasal length; nasal capsules nearly spherical; total vertebral counts 146–168 (6); and DP/MP ratio 1.6–1.8.

Ctenacis is compared with *Gollum* in the account of the latter genus below.

Triakis and *Mustelus* differ from *Ctenacis* in having external, transitional, or internal nictitating lower eyelids; no gill rakers or buccal papillae; anterior nasal flaps elongated and lobate; posterior nasal flaps absent or rudimentary; labial furrows long and extending well onto upper and lower jaws; lower teeth towards ends of dental band not comblike, with cuspules reduced or absent; roots of teeth usually subdivided on their attachment surface by a transverse groove and notch; interdorsal ridge present; longest distal radials of pectoral fin skeleton about as long as longest proximal radials or slightly longer; midpoint of first dorsal fin base about equidistant between pectoral and pelvic bases or definitely closer to pectoral bases; anal insertion slightly posterior to second dorsal insertion; anal posterior margin concave to deeply notched in adults; cranium with a deep notch separating the anterior end of the suborbital shelf from the nasal capsule (fig. 3); postorbital process exserted from the supraorbital crest and bifurcated distally; and vertebral centra with wedge-shaped intermedia.

In addition *Triakis* (including only *T. scyllium*, *T. semifasciata*, *T. maculata*, *T. acutipinna*, and probably '*Mustelus*' *megalopterus* and '*M.*' *nigropunctatus*) differs from *Ctenacis* in having an arcuate mouth (fig. 4C); fewer tooth rows, 44–65/34–56; and a well developed ventral caudal lobe in adults. *Mustelus* (including '*Triakis*' *henlei*) also differs from *Ctenacis* in having a longer snout, with a narrowly parabolic to almost angular shape in dorsoventral view and narrowly wedgelike shape in lateral view; teeth extending onto sides and ventral surface of lower jaw; teeth forming a regular pavement, with primary cusp typically reduced or absent in most species; a tooth peg present on the inner face of the crown; and ectethmoid condyles present on the nasal capsules.

DERIVATION OF NAME. *Ctenacis*, from Greek *ktenos*, comb, and *akis*, point (feminine), in allusion to the comblike posterior teeth of this genus.

SPECIES. Only one, *Ctenacis fehlmanni* (Springer, 1968).

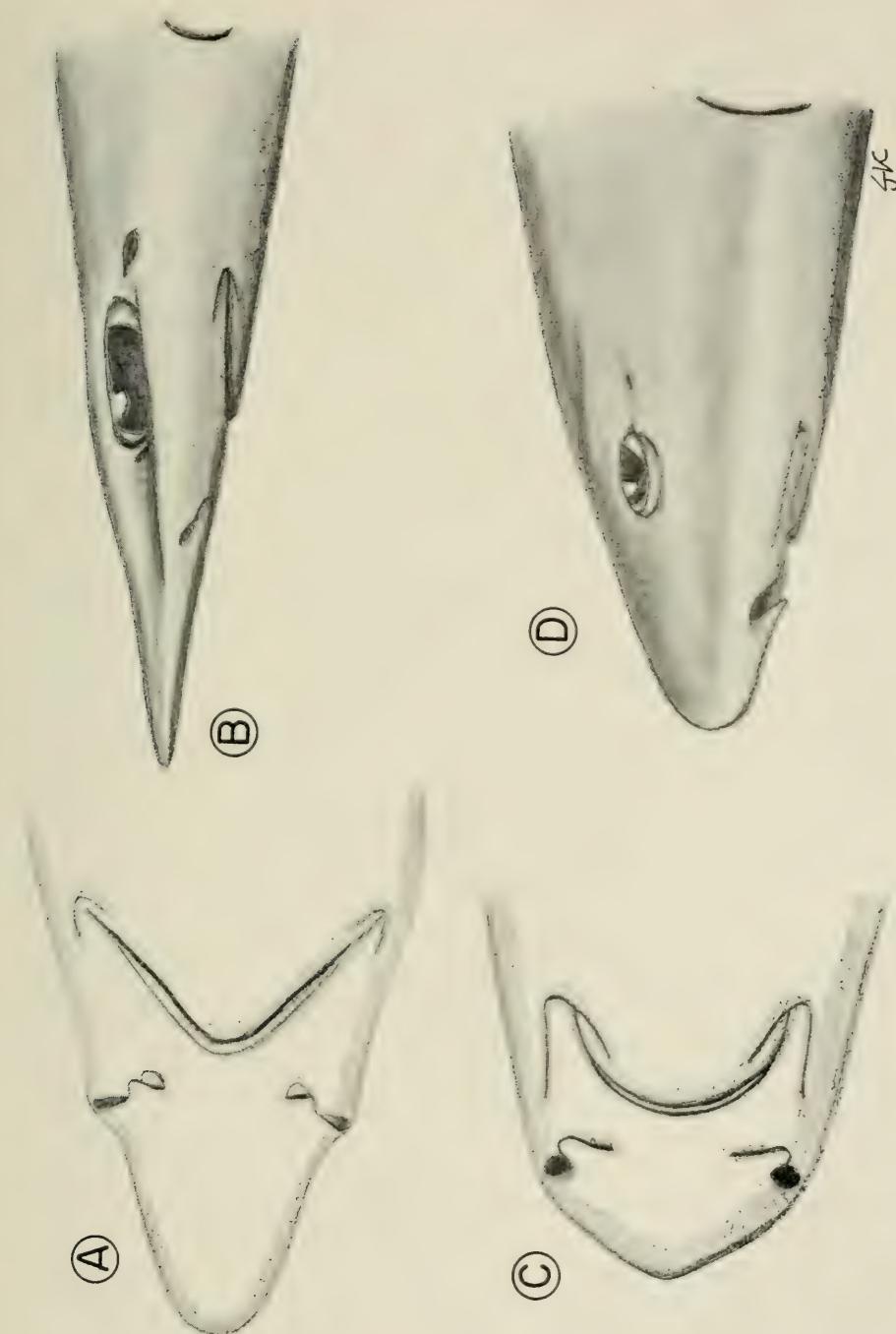
STUDY MATERIAL. The holotype and only known specimen of *Ctenacis fehlmanni*, U. S. National Museum 202969.

Gollum Compagno, new genus

TYPE SPECIES. *Triakis attenuata* Garrick, 1954.

DEFINITION. Head very broad, depressed, its length about $\frac{1}{5}$ (21.3–21.6 percent) of total length in adults. Head length considerably shorter than distance

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FIGURE 4. A–B, *Gollum attenuatus*, DM-4841, 1015 mm. adult female. Prebranchial head in ventral (A) and lateral (B) views. C–D, *Triakis scyllium*, University of Michigan Museum of Zoology 179067, 700 mm. immature male. Prebranchial head in ventral (C) and lateral (D) views.



between pectoral and pelvic bases. Snout with peculiar bell-shaped outline in dorsoventral view (fig. 4A). Snout very long, preoral length 8.4–8.6 percent of total length in adults. Eyes high on sides of head, above level of nostrils by a space equal to about half eye height or slightly less. Subocular ridge very strong, with a distinct depression on its dorsal surface (fig. 4B). Eyes not visible in ventral view. Eyes elongate-elliptical, with their apertures about $2\frac{1}{4}$ to $2\frac{1}{2}$ times as long as high. Nictitating lower eyelid rudimentary, with its edge horizontal. Subocular pouch very shallow and covered with denticles.

Spiracles present, their length about 3.8 to 8 times in eye length. Shortest gill opening $\frac{3}{4}$ to $\frac{5}{6}$ as long as longest one. No gill rakers.

Intermarial space about 1.8 to 1.9 times nostril width. Anterior nasal flaps short and subtriangular, not tubular or barbel-like, with edges entire and not fringed. Posterior edges of anterior nasal flaps close to mouth but separated from the upper symphysis by distance equal to $\frac{1}{2}$ to $\frac{3}{4}$ of nostril width. Posterior nasal flaps large, with fringed edges. Nasoral grooves absent.

Mouth distinctly angular in shape, with edges of lower jaw straight. No large papillae in buccal cavity. Labial furrows very short, essentially confined to mouth corners.

Dignathic heterodonty weak, virtually absent at symphysis but increasing towards ends of dental bands, where lower teeth are more comblike than uppers. No disjunct monognathic heterodonty. In both jaws teeth decrease in size and height relative to root width toward rictuses. In the lower jaw premedial cusplets increase in number and size relative to the primary cusp and the cusp shifts postlaterally on the crown in a direction towards the rictus, producing comblike posterior teeth. Gynandric heterodonty absent.

Tooth rows 96–99/108–114 (3), series functional 3–6/3–7. Crown not sharp, serrated, or bladelike. Premedial and postlateral cusplets present on all teeth. Primary cusp present on all teeth, narrow and erect. Crown foot with a deep basal ledge overlapping a deep basal groove. Transverse ridges present on teeth, numerous and small, extending onto primary cusp and cusplets. Roots of teeth moderately high and deep, not subdivided on their attachment surface by a transverse groove and notch. Teeth not extending onto sides and ventral surface of lower jaw.

Interdorsal ridge present. No lateral dermal keels or precaudal pits present on the caudal peduncle. Length of head and trunk about equal to tail length.

Denticles from sides of body below first dorsal fin with crowns much longer than wide in adults. Denticle crowns with a strong medial cusp, a strong medial ridge or a pair of medial ridges, a pair of short but strong lateral cusps, and a pair of lateral ridges.

Pectoral fin skeleton projecting slightly less than $\frac{1}{3}$ of pectoral anterior margin length into fin. Longest distal radials of pectoral skeleton somewhat

shorter than longest proximal ones. Distal radials with parallel edges and truncate tips.

Pelvic fin bases slightly closer to second dorsal base than to first dorsal base. Pelvic posterior margins, free rear tips, and inner margins not attenuate.

Dorsal edges of clasper groove not fused together between apopyle and hypopyle. A soft-edged, fleshy rhipidion present, with its dorsal surface exposed for most of its length and not concealed by the cover rhipidion. Cover rhipidion present, a small, short, square, fleshy flap. Exorhipidion present, a low, fleshy flap lateral to pseudopera. Exorhipidion without clasper hooks. A large pseudosiphon and pseudopera present.

Midpoint of first dorsal base about 1.3 times as far from pelvic bases as from pectoral bases. Free rear tip of first dorsal well anterior to pelvic origins.

Second dorsal fin about as large as first, its height equal or slightly larger than height of first dorsal, its base length equal or slightly less than base length of first dorsal. Posterior margin of second dorsal moderately concave.

Anal fin much smaller than second dorsal, its height 44–46 percent of first dorsal height, base length about $\frac{1}{2}$ to $\frac{3}{5}$ of second dorsal base. Anal origin posterior to second dorsal origin by distance equal to 11 to 27 percent of second dorsal base length. Anal insertion anterior to second dorsal insertion by distance about 25 to 36 percent of second dorsal base length. Anal posterior margin nearly straight, not deeply concave or notched.

Caudal fin with ventral lobe poorly developed in adults. Postventral caudal margin not notched. Subterminal caudal margin about $\frac{3}{5}$ to $\frac{7}{10}$ of terminal margin. Caudal short, not tapelike, in adults about $\frac{1}{5}$ (19.4–21.2 percent) of total length. No lateral undulations in dorsal caudal margin. Terminal sector of caudal between 3 and 4 times in dorsal caudal margin. A weak supracaudal crest of enlarged, circular or oval-crowned denticles present along the anterior half of the dorsal caudal margin.

Cranium with lateral and medial rostral cartilages fused at their tips to form a tripod (fig. 2). Rostral node not yokelike, not penetrated by a rostral fenestra. Rostrum very long, length of medial rostral cartilage only 1.3 in nasobasal length. Distance between bases of lateral rostral cartilages about 2.7 times in length of medial rostral. Lateral rostrals with their bases far anterior to anterior fontanelle but with their dorsal edges connected to fontanelle by a low ridge.

Nasal capsule oval in shape, transversely elongated. Transverse width of capsule about 1.4 times its length. Greatest width across nasal capsules 1.4 in nasobasal length. Nasal aperture and nasal fontanelle broadly continuous with each other, the fontanelle not separated from the nasal aperture by a bridge of cartilage. Greatest width of nasal aperture about 5 times distance between nasal apertures. Ectethmoid chamber opening inside nasal capsule on its

posteroventral wall, with its aperture just above posterior edge of nasal fontanelle and not separated from the latter by a horizontal ledge beneath it. No true ectethmoid condyles, though a pair of low condyles are present on the posteroventral surfaces of the nasal capsules (but well lateral to the position of the ectethmoid condyles of carcharhinoid genera that have them). Subethmoid fossa absent. No separate ectethmoid foramen on the ventral surface of the nasal capsule.

Anterior fontanelle rhomboidal in shape, its greatest width only 7 times in nasobasal length. Cranial roof flattened between orbits.

No deep notch separating suborbital shelf from nasal capsule. Basal plate expanded just posterior to nasal capsules into a broad suborbital ledge, the least width across which is about 2.0 in nasobasal length. Arterial foramina on ventral surface of basal plate include a pair of small internal carotid foramina about half as far from each other as from each of the tiny stapedial foramina distal to them. Basal plate slightly arched, without keels.

Supraorbital crest present, with an arcuate lateral edge. Dorsal edge of crest extending well above level of cranial roof between orbits. Width across narrowest part of crest about 3.6 in nasobasal length. Postorbital processes narrow, exserted beyond supraorbital crest and sphenopterotic ridge, with tips not bifurcated. Suborbital shelf very wide, greatest width across shelves 1.4 in nasobasal length.

Otic capsules short, not greatly enlarged and inflated. Length of otic capsule about 4 in nasobasal length. Sphenopterotic ridge extending medial to sides of otic capsule.

Occipital condyles very small, without dorsal and ventral covering plates for base of vagus nerve.

Total vertebral counts 166 (2). MP centra 30.7, DP centra 35.6, and DC centra 33.7 percent of total counts. DP/MP ratio 1.16, DC/MP ratio 1.10. "A" ratio 129 to 141, "B" ratio 87 to 99. No stutter zone. Last few MP centra not greatly enlarged.

Vertebral centra without wedgelike intermedia or diagonal calcified lamellae. Notochordal canal rather large through apices of calcified double cones.

Valvular intestine with a spiral valve having about 11 turns.

Development ovoviparous (Kato, 1968; J. A. F. Garrick, personal communication).

Ground color brownish gray dorsally, lighter below. No color pattern.

Size small-medium, males mature at 932 to 955 mm. total length, females at 1015 mm.

COMPARISON WITH OTHER GENERA. *Gollum* belongs to Compagno's (1970) group of 'scyliorhiniform triakoids,' in which it is a singular and isolated member. *Ctenacis*, *Proscyllium*, and *Eridacnis* all differ from *Gollum* in having shorter snouts, only 4.3 to 6.7 percent of total length and not bell-shaped in dorsoventral

view; no concavity or depression on the dorsal surface of the subocular ridge; gill rakers present; internarial space only 0.5 to 1.2 times nostril width; large papillae present in buccal cavity; fewer tooth rows, 46–86/49–88; interdorsal ridge absent; pelvic bases much closer to first dorsal base than second dorsal base; midpoint of first dorsal base much closer to pelvic bases than pectoral bases; first dorsal free rear tip over or posterior to pelvic origins; no supracaudal crest of denticles; rostral cartilages much shorter, medial rostral length 3 to 4 in nasobasal length; no lateral condyle on posteroventral wall of nasal capsule; postorbital process not exserted from supraorbital crest; sphenopterotic ridge not medial to sides of otic capsule; and size smaller, not exceeding 700 mm. total length when adult.

In addition *Ctenacis* differs from *Gollum* in having the head longer than the distance between pectoral and pelvic bases; second dorsal insertion over the anal insertion; distance across narrowest part of supraorbital crest greater, 2.6 in nasobasal length; total vertebral count 136; vertebral centra with knoblike diagonal calcified lamellae; and a color pattern of dark blotches and spots. *Eridacnis* also differs from *Gollum* in having the head about equal to the distance between pectoral and pelvic bases or longer than it; posterior nasal flaps not fringed; gynandric heterodonty more or less developed, in males spikelike teeth present in one or both jaws at the symphysis; head and trunk considerably shorter than the tail; pelvic inner margins, free rear tips, and posterior margins elongate-attenuate; anal origin under second dorsal origin or slightly anterior to it; caudal very long, tapelike, with dorsal caudal margin 24 to 30 percent of total length; and total vertebral counts only 113 to 144. *Proscyllium* also differs from *Gollum* in having the shortest gill opening less than half as long as the longest; anterior nasal flaps very large, broadly triangular, and nearly reaching the upper symphysis; edges of posterior nasal flaps not fringed; head and trunk only 39 to 41 percent of total length; dorsal edges of clasper groove fused together between hypopyle and apopyle; exorhipidion very strong, with clawlike clasper hooks on its distal edge; first dorsal origin well posterior to pectoral free rear tip; anal origin slightly anterior to second dorsal origin; DP/MP ratio 1.6 to 1.8; knoblike diagonal calcified lamellae present in vertebral centra; development oviparous; and a color pattern of dark spots and bars present.

Triakis and *Mustelus* differ from *Gollum* in lacking a bell-shaped snout profile in dorsoventral view (fig. 4C); no concavity or depression in dorsal surface of subocular ridge (fig. 4D); nictitating lower eyelid external or transitional in young but usually transitional or internal in adults; anterior nasal flaps somewhat elongated; posterior nasal flaps rudimentary or absent; tooth roots low, with transverse groove and notch usually present; crowns of teeth towards ends of tooth band not comblike, with cusps and cusplets reduced or absent; longest distal radials of pectoral fin equal in length or somewhat longer than longest proximal radials; claspers without exorhipidion; anal fin insertion

slightly posterior to second dorsal insertion; anal posterior margin moderately concave to deeply notched; no supracaudal crest of denticles; rostrum shorter, length of medial rostral cartilage 1.9 to 4.4 in nasobasal length; bases of lateral rostral cartilages not connected to edge of anterior fontanelle by a ridge; least distance across supraorbital crest 1.5 to 2.3 in nasobasal length; suborbital shelf separated from nasal capsule by a deep notch; no suborbital ledge between nasal capsule and suborbital shelf; postorbital processes bifurcated distally; sphenopterotic ridge above side of otic capsule or slightly distal to it, not medially situated; and vertebral centra with intermedia and diagonal calcified lamellae.

In addition *Triakis* differs from *Gollum* in having a thick short snout (fig. 4D), bluntly rounded or obtusely triangular in dorsoventral view (fig. 4C) and bluntly rounded in lateral view; an arcuate mouth; very long labial furrows extending along margins of upper and lower jaws; fewer tooth rows, 44–65/34–56; and a well developed ventral caudal lobe in adults. *Mustelus* also differs from *Gollum* in having a snout less acutely wedge-shaped in lateral view; labial furrows usually longer, extending well onto the upper and lower jaws; teeth forming a regular pavement, with primary cusps and cuspets reduced or absent in most forms; and a true ectethmoid condyle present on the nasal capsule.

DERIVATION OF NAME. *Gollum* (treated as a masculine noun), named for the antihero of J. R. R. Tolkien's *Lord of the Rings* trilogy, to whom this shark bears some resemblance in form and habits.

SPECIES. Only one known, *Gollum attenuatus* (Garrick, 1954).

STUDY MATERIAL. Dominion Museum (DM) 3636, 955 mm. adult male, from about 25 miles off Cape Brett, North Island, New Zealand; DM-4841, 1015 mm. adult male, off Karamea Bight, South Island, New Zealand.

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